Big-leaf mahogany *Swietenia macrophylla* population dynamics and implications for sustainable management

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Summary

1. The impacts of selective harvesting in tropical forests on population recovery and future timber yields by high-value species remain largely unknown for lack of demographic data spanning all phases of life history, from seed to senescence. In this study, we use an individual-based model parameterized using 15 years of annual census data to simulate population dynamics of big-leaf mahogany *Swietenia macrophylla* King in southeast Amazonia in response to multiple harvests and in the absence of harvesting.

2. The model is based on regression equations of stem diameter growth, mortality, and fruit production estimated as a function of stem diameter and prior growth; it includes functions for germinating seeds, growing trees from seedling to adult senescence, producing seeds, and creating disturbances at specified spatial scales and return intervals, including logging. We simulate six harvest scenarios by varying the minimum diameter cutting limit (60 cm, 80 cm) and the retention rate requirement (20%, 40% and 60% commercial population retained).

3. Without logging, simulated populations grew over 100 years by 182% from observed densities, indicating that one or more parameters in the model may overestimate long-term demographic rates on this landscape. However, 100-year densities did not far exceed values reported from forests across this region, and other modelled demographic parameters resembled observed behaviours.

4. Under current harvest regulations for mahogany in Brazil (60 cm minimum diameter cutting limit, 20% commercial-sized tree retention rate, minimum 5 commercial-sized trees 100 ha^{-1} retained after harvest, 30-year cutting cycle), commercial densities at the study site would decline from 39·7 to 11·3 trees 100 ha^{-1} before the fourth harvest in year 90, yielding an estimated 16·4% of the initial harvest volume during the fourth harvest. Increasing retention rates caused first-cut harvest volumes to decline but improved population recovery rates between harvests. Under both minimum diameter cutting limit scenarios, increasing retention rates led to more robust population recovery compared with the current 20% rate, and higher subsequent harvest yields relative to initial (first-cut) values.

5. *Synthesis and applications*. These results indicate that current harvest regulations in Brazil for mahogany and other high-value timber species with similar life histories will lead to commercial depletion after 2–3 cutting cycles. Increasing commercial-sized tree retention rates improved population recovery at the cost of reduced initial harvest volume yields. Sustainable harvests will require, in combination, a moderate increase in the retention rate, investment in

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artificial regeneration to boost population recovery, and implementation of silvicultural practices designed to increase growth rates by future crop trees.

Key-words: Amazon, Brazil, growth autocorrelation, growth modelling, individual-based model, sustainable forest management, tropical timber

Introduction

Big-leaf mahogany *Swietenia macrophylla*'s listing on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) requires verification that exported volumes were obtained legally and without detriment to natural populations (Blundell 2004). For timber species, 'non-detriment' is generally equated with sustainable forest management (Smith *et al*. 2011). In biological terms, sustainable harvests require that current harvest rates do not jeopardize population recovery and future harvests by crippling reproductive and regeneration capacity of surviving adult trees (Grogan *et al*. 2008; Schulze *et al*. 2008a,b). With passage of the 2006 Public Forests Law (Lei No. 11·284/ 2006) and associated forest policies, the Brazilian government committed to sustainable forest management as integral to conservation and development in the Amazon (Banjeree & Alavalapati 2010; Macpherson *et al*. 2010). Sustained production of timber and other products from public and private forests designated for this use is critical to current strategies for reducing illegal deforestation and logging. This would allow a network of effective reserve and timber production forests to be established, while providing sustainable economic opportunities for the millions of people living in the Brazilian Amazon (Nepstad *et al*. 2006; Araujo *et al*. 2009; Merry *et al*. 2009). In this paper, we examine whether current Brazilian management parameters for mahogany, the most valuable neotropical timber species, fulfil this commitment to sustainability as well as international regulations governing the harvest and commercialization of Appendix II species (Grogan & Barreto 2005).

Impacts of harvest practices on future timber yields can be simulated if empirical data are available to describe mortality, growth, and reproductive rates spanning a given species' life cycle. Demographic analysis may also need to account for other aspects of life history and landscape ecology, such as density-dependent mortality factors (Alvarez-Buylla & Martinez-Ramos 1992; Alvarez-Buylla 1994) and gap formation rates, especially for light-demanding tree species (Grogan & Galvão 2006b). Demographic analysis of tree population dynamics has traditionally relied on matrix models based on transition probabilities between life phases (Hartshorn 1975; Zuidema & Boot 2002; Gourlet-Fleury *et al*. 2005). Because this approach ignores variability between individuals of a given life phase and cannot incorporate growth autocorrelation, it may overestimate tree ages and the time required to reach reproductive maturity or commercial size (Pfister

& Stevens 2003; Landis & Peart 2005; Brienen, Zuidema & During 2006). To avoid this problem, we use an individual-based model for mahogany parameterized from field data collected from 1995 to 2010 in the Brazilian Amazon. The model is based on regression equations of stem diameter growth, mortality, and fruit production estimated as a function of stem diameter and prior growth; it includes functions for germinating seeds, growing trees from seedling to adult senescence, producing seeds, and creating disturbances at specified spatial scales and return intervals, including logging. The model incorporates growth autocorrelation which has been shown to strongly influence model predictions (Zuidema *et al*. 2009). Because the model is based on continuous relationships, we do not need to arbitrarily classify ('bin') the population into size categories; in matrix models, the choice of bin widths has been shown to substantially affect model predictions (Zuidema *et al*. 2010). By avoiding this problem, our modelling approach yields more realistic outcomes.

Uncertainty about mahogany's disturbance requirements for successful regeneration has been a major obstacle to the design of biologically based management systems. Researchers in Mexico and Bolivia have proposed that mahogany requires landscape-scale catastrophic disturbances such as hurricanes, fires or floods for seedling regeneration to occur at rates sufficient to maintain natural populations (Gullison *et al*. 1996; Snook 1996, 2003; Gullison, Vriesendorp & Lobo 2003). In the Amazon, mega-El Niño Southern Oscillation (ENSO) events proposed to be responsible for disruptions in the archaeological record at 400- to 500-year intervals over the past two millennia (Meggers 1994) could represent a stochastic mechanism maintaining mahogany populations at observed densities. However, observations of small-gap recruitment in southeastern Amazonia suggest that successful recruitment to the canopy occurs in the absence of large-scale disturbance and that the principal drivers of mahogany population dynamics may vary regionally (Brown, Jennings & Clements 2003; Grogan, Ashton & Galvão 2003).

We simulate mahogany population response to an observed forest canopy disturbance regime at the principal study site in southeast Pará, Brazil. We then simulate the impact of current Brazilian forest management regulations governing mahogany harvests over multiple cutting cycles; previous species-level modelling efforts have been constrained by data and model sophistication to simulating population recovery during a single cutting cycle (Grogan *et al*. 2008; Schulze *et al*. 2008a,b). Management regula-

tions were revised in 2003 to restrict harvests to trees > 60 cm diameter, to require retention of at least 20% of commercial-sized trees for seed and future timber production, and to bar logging where population densities are < 5 commercial-sized trees 100 ha^{-1} (Grogan & Barreto 2005). We simulate harvests by these guidelines at 30-year intervals over three cutting cycles (harvests in years 0, 30, 60 and 90) based on observed population structure and demographic behaviour. Finally, we adjust logging parameters to see whether increasing the minimum diameter cutting limit (MDCL) from 60 to 80 cm diameter or increasing the commercial-sized tree retention rate from 20% to 40% or 60% would yield higher commercial densities and volumes after repeated harvests. Outcomes reported here illustrate biological and operative problems common to many of the highest value timber species currently being harvested in the Amazon that share life history attributes with mahogany, including *Cedrela* spp., *Tabebuia impetiginosa* and *T. serratifolia*, and *Hymenaea courbaril* (Schulze *et al.* 2008a,b).

Materials and methods

STUDY SPECIES

Big-leaf mahogany is the most valuable widely traded tropical timber species. It is a canopy emergent tree associated with seasonally dry tropical forests from Mexico to Bolivia. Mahogany is a fast-growing, light-demanding late successional species (Lamb 1966). In southeastern Amazonia, its local distribution commonly traces seasonal streams or rivers; it occurs at highly variable but consistently low densities, up to 1·2 trees ≥ 20 cm diameter ha^{-1} (Grogan *et al.* 2008). The few published studies of growth and mortality of adult mahogany trees in natural forests are summarized by Grogan & Landis (2009).

STUDY SITE

The study site is a 4100-ha forest industry-owned management area called Marajoara, located at 7°50′S, 50°16′W in the southeast corner of the state of Pará (Fig. 1a). Climate is tropical dry. Annual precipitation during 1995–2001 averaged 1859 ± 82 mm (SE), with > 90% falling between November and May; in some years, no rain fell for 3–4 months during the dry season (Grogan & Galvão 2006b). Topographical relief is slight; all streams are seasonal within the principal research area of 2050 ha. The forest is dominated by evergreen trees intermixed with deciduous species. Marajoara was selectively logged for mahogany from 1992 to 1994, reducing landscape-scale densities from 0·65 to 0·19 mahogany trees ≥ 20 cm diameter ha^{-1} (Grogan *et al.* 2008). The site is surrounded by heavily logged and burned forest and pasture.

FIELD METHODS

The sample population at Marajoara consists of 358 mahogany trees > 10 cm diameter that survived selective logging within 2050 ha of the larger forest management area (Fig. 1b). These trees were censused annually between 1995 and 2010 for survival, stem diameter growth, and fruit production (see Grogan & Lan-

dis 2009 for detailed description of field methods). Due to selective logging prior to the study, mortality and growth rates may reflect a small post-logging increase (De Graaf, Poels & Van Rompaey 1999). Because few large mahogany trees survived logging at Marajoara, fruiting data for trees > 90 cm diameter were supplemented by observations from additional sites in southeast Pará as well as Acre, Brazil (southwest Amazonia, see Grogan *et al.* 2008) and Bolivia (Gullison *et al.* 1996). Demographic rates for trees < 10 cm diameter were estimated from seedlings (*N* = 237) grown from seed and planted into large (0·65-ha) artificial clearings opened within the study forest (Grogan 2001). This was necessary due to the scarcity of natural regeneration in gap environments. Nursery-grown seedlings were outplanted in 1996 and censused annually until 2010. These data present optimistic estimates of juvenile performance due to manual removal of competing vines and secondary vegetation during the first 3 years of the experiment; under these conditions, seedling survivorship ranged from 40% to 79% between the two clearings after 3 years.

The population diameter distribution used to initialize model simulations was based on a subset of 158 stumps and live trees ≥ 20 cm diameter that survived the initial harvest in 1992–1994, from a complete inventory in 204 ha (Fig. 1b). Densities of trees < 20 cm diameter were derived from stratified transect surveys in 1035 ha. See Fig. 2a for the resulting diameter size class distribution.

MODEL CONSTRUCTION

The mahogany population model was constructed and outcomes analysed using R version 2.13.2 (R Core Team 2012) including nlme, MASS and rms packages (Pinheiro & Bates 2000; Harrell 2001; Venables & Ripley 2002). The individual-based population model simulates trees over annual time steps. Similar to matrix-based models, the model does not explicitly model spatial processes nor does it incorporate density dependence. Unlike matrix-based models, it incorporates growth autocorrelation, the tendency for fast-growing trees to remain fast-growing, which has been shown to strongly influence modelling results (Brienen & Zuidema 2007; de Valpine 2009; Zuidema *et al.* 2009). Assumptions underlying model functions described below are based on published results from experimental and observational studies at Marajoara and on extensive field experience with mahogany across its wide range in Brazilian Amazonia.

A simulation begins with the population diameter distribution before logging at the study site (Fig. 2a). At each time step, the following demographic parameters are estimated for each tree based on regression equations derived from annual census data: (i) mortality probability, (ii) diameter increment (cm year^{-1}), (iii) probability of fruit production, and (iv) number of fruit produced. Diameter increment is estimated as a function of stem diameter using generalized least squares to incorporate an autoregressive error term, accounting for growth autocorrelation over the preceding 10 years (Pinheiro & Bates 2000; Grogan & Landis 2009). Mortality and fruiting probabilities are estimated as binary logistic regressions derived from current-year stem diameter and diameter increment. Fruit production is estimated as a function of current-year stem diameter in a generalized linear model with a negative binomial error term (Venables & Ripley 2002). Growth and fruit production values assigned to each tree both incorporate a stochastic component based on error terms derived from their respective regression models, incorporating uncertainty asso-
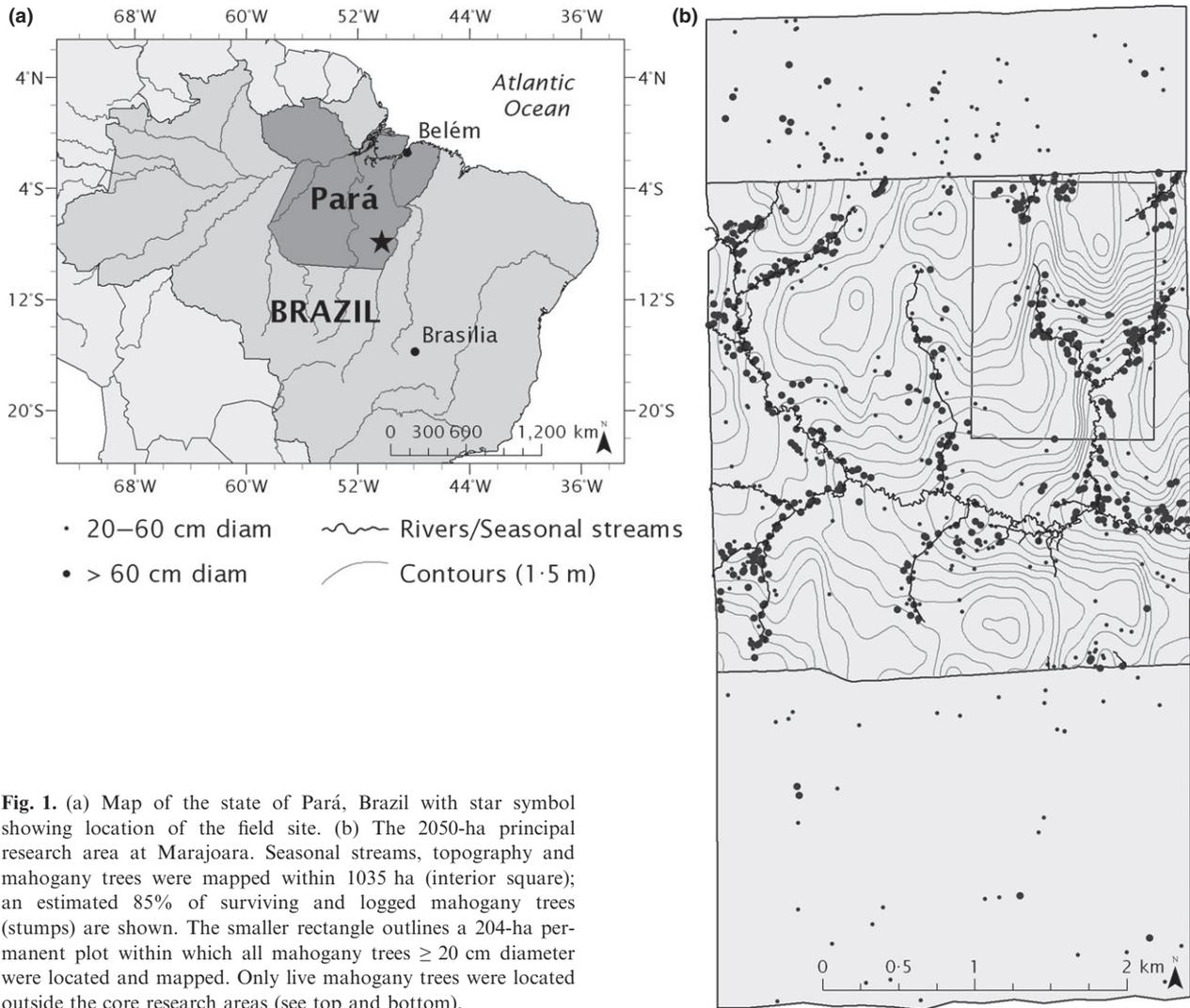
Fig. 1. (a) Map of the state of Pará, Brazil with star symbol showing location of the field site. (b) The 2050-ha principal research area at Marajoara. Seasonal streams, topography and mahogany trees were mapped within 1035 ha (interior square); an estimated 85% of surviving and logged mahogany trees (stumps) are shown. The smaller rectangle outlines a 204-ha permanent plot within which all mahogany trees ≥ 20 cm diameter were located and mapped. Only live mahogany trees were located outside the core research areas (see top and bottom).

ciated with respective statistical models into simulations. Functions and estimated regression coefficient values are provided in Table S1 (Supporting information). The resulting simulated relationships compared with observed data are shown in Fig. 2b–f.

Once fruit production is determined for surviving reproductive trees, new seedling recruits are added to the population according to the following equation:

$$1\text{-year-old seedlings} = \sum_{i=1}^{n} \text{fruit}_i * s_{\text{fruit}} * f_{\text{surv}} * f_{\text{gap}} * f_{\text{viable}}$$

where n is the number of reproductive trees in the population, fruit_i is the number of fruit produced by tree i, s_{fruit} is the mean number of viable seeds per fruit (42·4), f_{surv} is the fraction of seeds that germinate and survive to become 1-year-old seedlings (0·085), f_{gap} is the fraction of the landscape in canopy gaps exclusive of logging (0·026), and f_{viable} is the fraction of gap area viable for recruitment (0·618). The four constants are derived from observational data at Marajoara (Grogan & Galvão 2006a,b). Constants were used for these parameters in the absence of more detailed data; below, we explicitly examine the implications of changing values of constants we deemed most likely to affect model results, especially f_{surv} and f_{gap}. A uniform distribution of seeds within a 0·9-ha seed shadow was assumed for simplicity

(Grogan & Galvão 2006a). Initial seedling diameter growth rates are randomly drawn from observed empirical distributions. Based on field observations, we set the minimum gap radius for successful regeneration at 10 m, allowing seedling recruitment only in gaps larger than 314 m² (Grogan, Ashton & Galvão 2003; Grogan *et al*. 2005). Only seedlings growing in gaps are tracked in the model; seedlings in understorey locations are assumed to have 100% mortality prior to reaching reproductive age (Grogan *et al*. 2005). Gap size larger than the minimum viable recruitment area (314 m²) is assumed to have no effect on seed germination, early survival, and growth rate (Grogan & Galvão 2006a).

NATURAL GROWTH AND SENSITIVITY ANALYSIS

We ran 500 simulations of 100 years without logging to evaluate outcomes of the initial population under observed growth and disturbance regime conditions. To examine the sensitivity of population outcomes to demographic parameters modelled by the least robust data, we adjusted the disturbance rate (0·026), first-year seedling establishment rate (0·085), and seedling/sapling mortality rate by ±10%, 25% and 50%. Each sensitivity analysis was simulated 500 times for 100 years without logging.
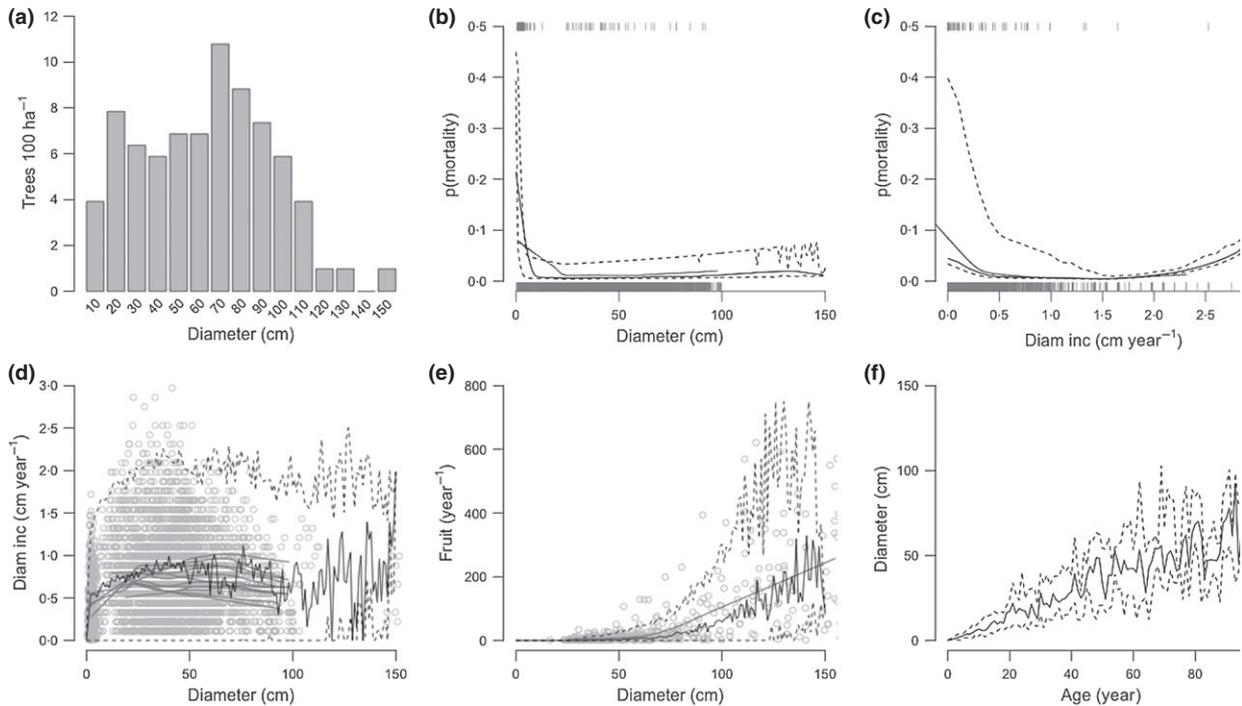
Fig. 2. Population characteristics of observed and simulated mahogany populations at Marajoara. (a) Initial population diameter size class distribution. (b) Probability of mortality as a function of stem diameter. (c) Probability of mortality as a function of diameter increment (growth) rate. (d) Diameter increment rate as a function of stem diameter. (e) Fruit production as a function of stem diameter. (f) Stem diameter as a function of age. In panels (b–d), black lines and dashed lines show median and 5th and 95th percentile simulated values, respectively, from a randomly selected simulation; grey lines show median observed values using LOWESS smoothers (for each year of measurement in d). In (b) and (c), observed data are shown as tic marks across panel tops (deaths) and bottoms (survivors). In (d) and (e), open grey circles show observed data points. No observed data are available for (f).

LOGGING SCENARIOS

Logging was implemented by randomly removing (harvesting) commercial-sized mahogany trees larger than the MDCL from the population. Logging was simulated under six scenarios defined in terms of MDCL (60 and 80 cm) and retention rate (proportion of trees > MDCL retained in the population: 20%, 40% and 60%). Each scenario was simulated 500 times for 100 years. Harvested trees were removed at the start of a model run (year 0) and every 30 years thereafter. Half of the logged trees were assumed to disperse seeds prior to felling based on the seasonal timing of logging in this region, which begins 2 months before seeds disperse during the middle of the dry season. Seedling recruitment gaps created by logged mahogany trees were sized proportionally to stem diameter based on empirical data from Marajoara (Grogan & Galvão 2006a). Treefall gaps created by harvesting secondary timber species are not available for regeneration purposes because (i) seed dispersal shadows cover a relatively small portion of landscapes where mahogany occurs (Grogan & Galvão 2006a), (ii) we have not observed mahogany regeneration in logging gaps created by felling secondary species (Grogan *et al.* 2005), and (iii) in most regions where mahogany persists, harvest intensity of secondary species will be low due to harvest and transportation costs (Veríssimo *et al.* 1995; Grogan, Barreto & Veríssimo 2002).

To estimate roundwood volumes, we used a single-entry equation from Kometter (2011) based on a large sample of mahogany trees in Guatemala:

$$V = -5·298 + 0·126 * D$$

where V = volume (m^3) and D = diameter (cm) at 1·3 m height on the bole.

DATA ANALYSIS

We validated the model using a pattern-matching approach (Grimm & Railsback 2005) by comparing simulated characteristics from 500 replicate runs of 100 years to actual tree characteristics observed over the 15-year study period at Marajoara. Simulations yielded realistic tree ages, diameters, and diameter growth rates both in terms of median and maximum values (Fig. 2, Fig. S1, Supporting information; see Dünisch, Montóia and Bauch 2003 for aged mahogany trees of comparable stem sizes). Because maximum fruit production outcomes exceeded observed values by as much as a factor of 2, number of fruit was capped at 750 to avoid unrealistically high values.

For each logging scenario, the median density of commercial-sized trees 100 ha^{-1} among 500 model runs was calculated along with 5th and 95th percentiles. Data are presented as number of trees 100 ha^{-1} because forest management operations in the Brazilian Amazon are typically implemented in 100-ha blocks. This unit area is easy to visualize – a square with sides of 1 km – and permits density measures to represent whole rather than fractional trees.

The density of commercial-sized trees and diameter distributions after 100 years were recorded from each simulation for comparison with initial values. The density before and after each harvest within a given simulation was recorded to evaluate recovery rates, while the volume of each harvest was recorded to track harvest productivity and volume recovery. The proportion of harvests in which the population was logged to the minimum density was recorded at each harvest interval in all scenarios.

Results

MATCH OF SIMULATED TO OBSERVED DATA

Median simulated demographic values closely resembled median long-term observed values at Marajoara (Fig. 2b–f). The range of simulated values (5th and 95th percentiles) also fell within observed values in most cases. The wide range of simulated outcomes for diameter increment and fruit production as a function of stem diameter were derived from incorporation of stochastic error terms in model algorithms. Areas where the model underperformed compared with observed values include overestimation of mortality at small stem sizes (Fig. 2b), underestimation of mortality at slow diameter increment rates (Fig. 2c), and underestimation of fruit production rates across middle stem diameter sizes (Fig. 2f).

SIMULATED MAHOGANY POPULATION DYNAMICS

Under observed demographic and landscape-scale disturbance parameters, mahogany population densities (trees ≥ 20 cm diameter) declined briefly and then increased steadily over the course of 100-year simulations without logging (Fig. 3). Initial declines were due to the scarcity of pole-sized and seedling advance regeneration at Marajoara. Seedlings establishing in year 0 in gaps sufficiently large for recruitment to adult size required 20–30 years to enter the population of trees ≥ 20 cm diameter. New recruits in turn required 60–70 years to reverse the gradual mortality-related decline in density by commercial-sized trees. The median density of trees ≥ 20 cm diameter increased from 65·7 to 185·3 trees 100 ha^{-1} during 100-year simulations, an increase of 182%. The median density of trees > 60 cm diameter increased from 39·7 to 44·6 trees 100 ha^{-1} in year 100 (12% increase), the lower expansion rate due to delayed recruitment into larger diameter size classes.

MODEL SENSITIVITY

Varying the disturbance, first-year seedling establishment, and seedling/sapling mortality rates by ±10%, 25% and 50% yielded equivalent percentage changes in simulated population outcomes over 100-year periods for trees ≥ 20 cm diameter (Fig. S2, Supporting information). Because these rates vary over time in response to external factors including forest structural development patterns
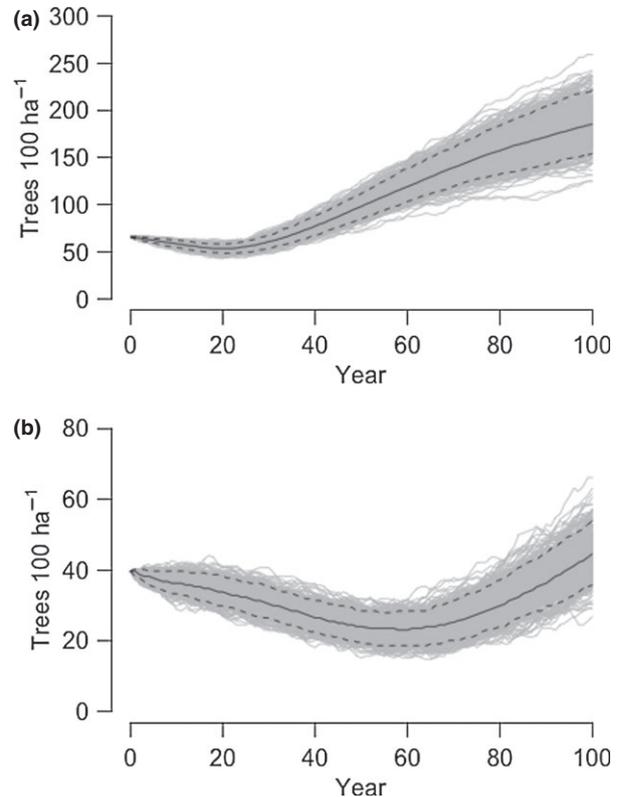

Fig. 3. Simulated mahogany population dynamics at Marajoara in the absence of logging; see Fig. 2a for initial size class frequency distribution. (a) The density of trees ≥ 20 cm diameter during 100-year simulations. (b) The density of trees > 60 cm diameter (commercial size) during 100-year simulations. Grey lines indicate 500 replicate runs, the solid black line indicates the median value, black dashed lines indicate 5th and 95th percentiles.

and long-term meteorological trends, static rate values derived from short-term observational and experimental studies represent primary sources of error in simulated outcomes.

HARVEST SIMULATIONS: CURRENT LEGAL STANDARDS

Brazilian forest management regulations governing mahogany production were revised in 2003 to restrict harvests to trees > 60 cm diameter, to require retention of at least 20% of commercial-sized trees for seed and future timber production, and to prohibit logging where population densities are < 5 commercial-sized trees 100 ha^{-1} (Grogan & Barreto 2005). Median outcomes from 500 simulated harvests by these guidelines at 30-year intervals over three cutting cycles (harvests in years 0, 30, 60, and 90) indicate that commercial-sized tree densities would decline from 39·7 trees 100 ha^{-1} in year 0 to 13·7, 8·8 and 11·3 trees 100 ha^{-1} in years 30, 60 and 90 after population recovery during the first, second and third cutting cycles, respectively (Fig. 4 and Table S2, Supporting information). These densities represent 34·6%, 22·2% and 28·4% of initial commercial densities. All model runs were

logged to the minimum commercial density during second, third and fourth harvests. Declines in roundwood production rates were sharper: median estimated harvest volumes during second, third and fourth harvests represented 26·3%, 10·1% and 16·4%, respectively, of production during the initial harvest in year 0 (Table S3, Supporting information). This was due to a reduction in the average commercial tree size over the course of four harvests.

HARVEST SIMULATIONS: ALTERNATIVE SCENARIOS

We adjusted logging parameters to determine whether increasing MDCL or increasing the commercial-sized tree retention rate would yield higher population densities and harvest volumes over repeated harvests. For 60 cm MDCL, increasing the retention rate to 40% and 60% doubled and tripled post-harvest commercial population densities in year 1 immediately after the first harvest compared with 20% retention and yielded larger commercial populations in year 90 (median densities 15·7 and 21·1 trees 100 ha^{-1}, respectively), with recovered populations representing 39·5% and 53·1% of initial commercial densities (Fig. 5 and Table S2, Supporting information). Commercial population recovery accelerated markedly during the third 30-year cutting cycle (years 61–90) as seedling recruits establishing in year 0 entered the commercial size class. The minimum harvestable density of 5 trees 100 ha^{-1} became less of an issue at higher retention rates, limiting harvests only in the 60 cm–40% retention scenario during some simulations in years 60 and 90. Although the estimated harvest volume in year 1 at 60%
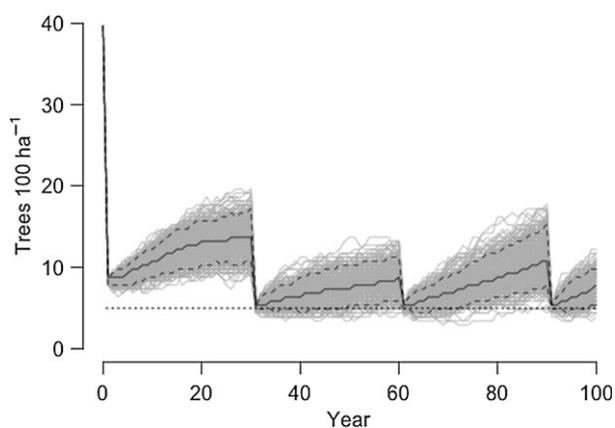

Fig. 4. Simulations of mahogany population dynamics in southeast Pará, Brazil under current legal harvest regulations: 60 cm minimum diameter cutting limit (MDCL), minimum 20% commercial-sized tree retention rate, 5 trees 100 ha^{-1} minimum post-harvest commercial population density, and (25- to) 30-year cutting cycles. There were 39·7 commercial-sized trees 100 ha^{-1} in year 0. Grey lines indicate 500 replicate runs, the solid black line indicates the median value, black dashed lines indicate 5th and 95th percentiles, and the horizontal dotted line indicates the minimum post-harvest commercial density. Median recovered population densities in years 30, 60 and 90 before successive harvests were 13·7, 8·8 and 11·3 trees 100 ha^{-1}.

retention declined by half compared with 20% retention (83·0 vs. 165·5 m^3, respectively), median summed harvest volumes over four harvests fell by only 18·2% (208·2 vs. 254·4 m^3; Fig. 5 and Table S3, Supporting information), with consistently higher harvest volumes during successive harvests at higher commercial retention rates.

Increasing MDCL to 80 cm under the 20% retention rate reduced the number of commercial-sized trees in year 0 by 49% to 20·1 trees 100 ha^{-1}. The corresponding reduction in harvestable volume in year 0 (by 37·6%, from 165·5 to 103·3 m^3; Table S2, Supporting information) was less extreme because the largest trees contributed disproportionately to harvest volumes. Roundwood yields were restricted by the minimum density requirement during all harvest years in the 80 cm–20% retention scenario, and estimated summed production was 19·4% less than in the 60 cm–20% retention scenario (254·4 vs. 205·2 m^3; Table S3, Supporting information).

Increasing retention rates to 40% and 60% under 80 cm MDCL yielded similar population outcomes after three cutting cycles, with median densities of 8·8 and 9·8 trees 100 ha^{-1} in year 90 immediately prior to the fourth harvest, respectively, compared with 7·8 trees 100 ha^{-1} at 20% retention. At these commercial densities, the minimum density requirement restricted median estimated fourth-harvest volumes to 18%, 29% and 52% of initial harvests in year 0 at 20%, 40% and 60% retention rates, respectively.

For both simulated MDCL, the 20% retention rate yielded the highest volume production summed over four harvests but the lowest 90-year volume recovery rate as a percentage of year 0 harvests.

Discussion

Our individual-based model approximates mahogany population dynamics at the study site in southeastern Amazonia based on field data collected over a 15-year period. Consistent expansion of the initial observed population over 100-year simulations without logging (Fig. 3) suggests that one or more parameters in the model may overestimate long-term abiotic or demographic rates on this landscape. The constant value assumed for landscape-scale disturbance inadequately describes an important dynamic factor shaping mahogany population dynamics. Another likely candidate is early seedling demography: because we use outplanted nursery-grown seedlings as the basis for this function, the survival rate used in the model is probably higher than for naturally established seedlings. And the lack of density-dependent mechanisms in the model to account for two known mahogany seedling and sapling predators, the moths *Steniscadia poliophaea* and *Hypsipyla grandella* (Grogan & Galvão 2006a; Norghauer *et al.* 2006, 2010), may also contribute to simulation outcomes. In spite of these limitations, modelled demographic relationships closely match observed relationships (Fig. 2) and the median projected density after 100 years
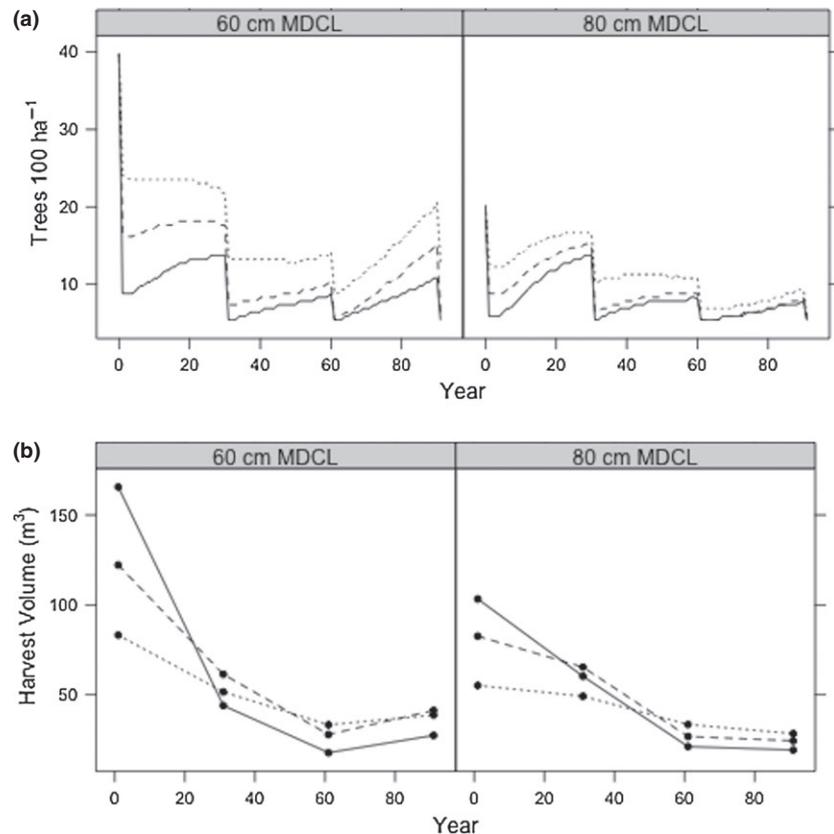
Fig. 5. Simulations of mahogany population dynamics in southeast Pará, Brazil, under six different logging scenarios defined by harvest regulations as in Fig. 4. For each scenario, 500 replicate runs were performed; lines show median values. In year 0, there were 39·7/20·1 commercial-sized trees 100 ha^{-1} in MDCL = 60 cm/ 80 cm scenarios, respectively. (a) Median population densities by minimum diameter cutting limit (MDCL) under three retention rates: 20% (solid lines), 40% (dashed lines) and 60% (dotted lines). (b) Estimated harvest volumes (m^3) from simulations in (a). See text and Tables S2 and S3 (Supporting information) for numerical outcomes.

(186 trees 100 ha^{-1}) does not far exceed landscape-scale densities reported from this region (up to 118 trees 100 ha^{-1}; Grogan *et al.* 2008), comparable to densities reported from Mato Grosso (178 trees > 40 cm diameter 100 ha^{-1}; Dünisch, Montóia & Bauch 2003). For these reasons, we are confident that the model is sufficiently robust for the purpose of harvest simulations on timeframes considered here; reported outcomes are likely to err on the side of optimism.

Simulations indicate that current harvest regulations designed specifically for mahogany in Brazil will lead to population decline and commercial depletion within 3–4 cutting cycles (60–90 years) where populations lack sub-commercial trees at densities sufficient for short-term replacement (Grogan *et al.* 2008; Schulze *et al.* 2008a,b). Without strict adherence to the minimum density requirement of 5 commercial-sized trees 100 ha^{-1}, few commercial-sized trees will survive after four harvests. Reducing logging intensity by increasing the MDCL from 60 to 80 cm and/or increasing the commercial tree retention rate from 20% to 40% or 60% would boost commercial densities and estimated harvest volumes during successive harvests, but at the cost of sharply reduced year 0 production and lower cumulative production. Reported outcomes are likely to overstate post-harvest recovery rates by surviving mahogany populations in Brazil, which are concentrated in southwest Amazonia and are characterized by lower densities of sub-commercial stems relative to commercial-sized trees compared with populations in

southeast Amazonia like Marajoara's (Grogan, Barreto & Veríssimo 2002; Grogan *et al.* 2008, 2010).

Like any regression-based model, conclusions drawn here are based on the data available, which limit our ability to extrapolate to other sites and to conditions for which we have no observations, such as higher population densities typical in Mexico and Central America. Whether model functions are transferable to mahogany populations beyond southeast Pará will depend on the degree to which basic demographic rates vary geographically. While published data are scarce, mahogany mortality, diameter increment, and fruit production rates appear relatively consistent across its natural range (Gullison *et al.* 1996; Dünisch, Montóia & Bauch 2003; Snook, Cámara-Cabrales & Kelty 2005; Grogan & Galvão 2006a; Shono & Snook 2006; Grogan & Landis 2009). Key limitations of the model stem from the lack of robust data for values such the disturbance regime, which varies considerably across mahogany's range, and early seedling demography. Addressing these limitations will be expensive and time-consuming and are unlikely to be forthcoming in the near future. In the absence of such data, our model based on long-term observations at Marajoara provides the best estimates of mahogany population dynamics currently available.

Two key aspects of mahogany life history at the study site largely explain simulation outcomes: (i) low densities of sub-commercial relative to commercial-sized trees (Fig. 2a) mean that commercial population recovery

under observed demographic parameters is delayed by 60–70 years or more after logging (Fig. 3) and can only occur if seedlings are in place in the forest understorey at the time of logging or establish in sufficient numbers at the time of first harvest for population replacement. The scarcity of seedling advance regeneration at Marajoara is a condition consistently encountered at research sites across the southern Brazilian Amazon (Veríssimo *et al.* 1995; Simões 1997; Grogan, Ashton & Galvão 2003; Grogan *et al.* 2003, 2008). (ii) Annual mortality of sub-commercial and retained commercial-sized trees means that population and volume recovery between harvests is slowed even at retention rates as high as 60%.

Restoring populations to historic densities and creating sustainable management systems will depend on successful recruitment by seedling regeneration in place or establishing at the time of logging, or established through enrichment planting in logging gaps (Lopes, Jennings & Matni 2008; Navarro-Cerrillo *et al.* 2011). Because background densities of mahogany regeneration are generally very low in natural forests, post-logging enrichment planting with active long-term manual tending to ensure seedling survival and robust growth must accompany mahogany harvests for the CITES non-detriment provision to be met (Grogan *et al.* 2005; Navarro-Cerrillo *et al.* 2011). This approach, in combination with reduced-impact logging (RIL) systems designed to reduce damage to residual stands and increase operational efficiency (Uhl *et al.* 1997; Barreto *et al.* 1998), has been implemented since 2012 on an experimental basis in the only forest management plan that includes mahogany currently operative in Brazil (R. Oliveira, personal communication). Silvicultural interventions opening canopy and understorey growing space beyond levels expected under RIL have been shown to improve post-logging regeneration densities and growth rates by mahogany and similar species (Fredericksen & Putz 2003; Peña-Claros *et al.* 2008; Verwer *et al.* 2008). However, mahogany's low commercial densities in remote southwestern Amazonian forests where most unlogged populations survive, combined with generally low densities and market values of associated secondary timber species, indicate that the most cost-effective way to ensure future harvests will be to invest intensively in establishing and tending artificial regeneration rather than extensively to promote natural regeneration which is scarce to begin with.

Other high-value tropical timber species with life history, density and population dynamics similar to mahogany's, such as Spanish cedar *Cedrela odorata* and ipê *Tabebuia* spp., experience higher exploitation rates than those allowed for mahogany. Current legal harvest practices for these species are likewise unsustainable and must be revised to account for species biology (Schulze *et al.* 2008a,b). Regulatory policies requiring that internationally traded volumes be legally harvested without detriment to local populations must acknowledge biological 'facts on the ground' rendering current legal frameworks unsustainable.

Sustainable management of mahogany and other high-value Amazonian timber species is technically feasible, but will require greater financial investment than is commonly acknowledged. Whether through costs associated with reduced harvest intensity or investments in artificial regeneration, sustainable management of these species will be more expensive than current best practices (Verwer *et al.* 2008). Research suggests that successful artificial regeneration of high-value timber species will reduce but not eliminate overall profitability of management operations (Schulze 2008; Keefe *et al.* 2009). While the question of who should bear the financial costs of sustainable management remains unresolved, we show here that the biological constraints on sustainable management are much more certain.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Mahogany population model functions.

Table S2. Simulated densities of commercial-sized trees 100 ha^{-1} during three cutting cycles (four harvests) at Marajoara, harvesting in years 0, 30, 60, and 90 with 30-year recovery periods.

Table S3. Simulated roundwood volume production rates (m^3 100 ha^{-1}) during three cutting cycles (four harvests) at Marajoara with 30-year recovery periods.

Fig. S1. Maximum values for life history characteristics of simulated mahogany trees in southeast Pará, Brazil.

Fig. S2. Sensitivity analysis of model parameters.